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Research article

Climate limits on European forest structure across space and time

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ABSTRACT

The structure of a forest dictates its function, vulnerability to mortality, and ecosystem services it provides. Many aspects of the environment and management determine forest structures, such as canopy height, stand density, carbon content, etc. Environmental factors, such as climate, limit the extent to which management can maximize structures of a forest. By understanding how climate limits forest structures over large landscapes we can better quantify the potential upper limit that a forest structure can achieve independent of management. Further, by quantifying how climate limits forest structures we can deepen our understanding of the impact climate change has had and will have on our forest resources and services. This type of information goes beyond quantifying how climate will impact the pools and fluxes of a forest, which is typically done for climate change studies over large landscapes. Estimating how climate change will impact structures will allow us to quantify how climate change will impact resources and services unquantifiable by pools and fluxes alone – such as biodiversity, habitat suitability, and market values. We quantified how maximum and minimum temperatures, and precipitation limit 3 forest structures, diameter at breast height, height, and basal area across the European continent. We found that climate zones exist that maximize each forest structure. Further, we estimated how climate change since the 1950's has influenced the potential structures of European forests by assessing eight individual forests throughout Europe and then Europe as a whole. All three forest structures are limited in different ways depending on their location in Europe. Though some individual forests have seen a benefit from climate change, European forests on average have lost 5.0%, 1.7% and 6.5% of potential forest diameter, height and basal area respectively. Further, the extremes of the climate values in our study, which may support endemic life, have already begun to vanish from the entire continent.

1. Introduction

Forests are a crucial component of the global carbon cycle (Pan et al., 2011), essential in maintaining biodiversity (Cardinale et al., 2012), and providing ecosystem services that benefit human wellbeing (Millennium Ecosystem Assessment, 2005). Current and future changes in climate (Easterling, 2000; Luterbacher et al., 2004; IPCC, 2013) have and will affect forests worldwide by varying degrees, both positively and negatively (Idso and Kimball, 1993; Cramer et al., 2001; Parmesan and Yohe, 2003; Schröter et al., 2005; Oren et al., 2006; Norby et al., 2010). Climate change, however, does not occur consistently spatially or temporally (Katz and Brown, 1992; Easterling, 2000; Luterbacher et al., 2004; IPCC, 2013).

The relationship between climate and forest dynamics has been studied extensively across large-scales, in terms of impact on carbon storage (Larjavaara and Muller-Landau, 2012; Keith et al., 2009; Saatchi et al., 2011; Thurner et al., 2014), forest productivity (Melillo et al., 1993; Zhao and Running, 2010; Kolby Smith et al., 2015), tree mortality and disturbance regimes (Dale et al., 2001; Seidl et al., 2014). However, the influence climate has on forest structure, such as diameter at breast height (DBH), tree height or basal area remains understudied. Some research has been done to understand the affect temperature has on height but not in a spatially explicit manner and not allowing for the influence precipitation also has on height (Larjavaara, 2014). This paucity of research activity is potentially due to challenges in modelling forest structural characteristics on large scales, or lack of access to or availability of data over large enough areas to quantify effects. Various forest stakeholders require information on forest structures beyond total productivity and carbon stock to quantify various forest properties including biodiversity (Lindenmayer et al., 2000; Pardini et al., 2005), disturbances mitigation (Wilson and Baker, 1998; Dale et al., 2001) and the value of timber within a forest. Forest structures are typically used to quantify the resources and services a forest provides. Forest owners, politicians and the general population may be more interested in how

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climate change will affect resources and services, as defined by forest structures, than how it will impact more esoteric concepts such as vegetation indexes, fluxes and pools. For this reason, it is important to understand the structural limitations, if any, that climate has on forests and how a changing climate will impact these structures (Shore et al., 2003; Bekker and Taylor, 2010; Seidl et al., 2011).

While many organisms have the potential to respond to changing climate conditions by migration (Berry et al., 2002), forests have limited capabilities for migration and must adapt to local conditions (Smith et al., 2008; Ohlemüller, 2011; Wiens et al., 2011). Though species as a whole may be capable of migration as has been done in the past over appropriate timescales, individual forests with established structures cannot relocate (Mclachlan et al., 2005). Altered environmental envelops of tree species may have large impacts on the ecosystems such as is the case of older high elevation forests shifting to new forest types (Dullinger et al., 2012; Pauli et al., 2012). Empirical observations indicate that these species and forest type shifts are already evident (Kelly and Goulden, 2008). Forest structures take decades or even centuries to develop, so shifting species do not equate to an immediate or equal shift in forest structures.

Forest ecosystems respond to changing environmental conditions by transitioning to different forest types when certain thresholds are exceeded (Satake and Rudel, 2007; Bolte et al., 2009). Such forest transitions often exhibit a non-linear behavior, hysteresis or multiple equilibria (Hirota et al., 2011; Scheffer et al., 2012). An often cited example of such a shift in forest type, and thus forest structure, is from closed canopy forests to open savannah-like woodland and vice versa (Johnson and Risser, 1975; Mayle and Langstroth, 2007; Scheffer et al., 2012). Such transitions can have repercussions on local economies and ecosystem services as well as global carbon dynamics and biodiversity.

European forests contain approximately one-third of the world's temperate forest biomass (Pan et al., 2011). Societies in Europe rely on the continual provision of ecosystem services provided by forests for their economic, social and environmental sustainability (FOREST EUROPE, 2015). However, the large-scale impact of long-term climate conditions on forest structure in Europe remains understudied due to lack of accessible forest structure data. Recent work on linking remotely sensed data with European forest inventory data (Neumann et al., 2016a) has permitted the creation of a new pan-European forest structure data set. This data along with newly downscaled European historic climate data (Moreno and Hasenauer, 2015) allows analysis on how long-term climate conditions have affected forest structure on the continental scale. In this study, we quantify the absolute biophysical limits climate places on forest structure, both generally and spatially, and how climate change has affected potential forest structure on local and continental scales.

2. Material and methods

2.1. Overview

We spatially and temporally assessed how climate limits forest structure on the individual forest and continental scale throughout Europe using only empirical observations on forest structure and climate. We derived general forest structure potential upper limit response curves and climate space plots to individual climate variables and combinations of climate variables respectively. Using climate space plots, we assessed how changes in climate affect eight specific forests in Europe from the 1950's to present. We then used the climate response curves to derive pan-European geographic maps of potential upper limit forest structure values, i.e., maps of the upper limits of DBH, height and basal area. Finally, we analyzed how a changing climate affects forests on the continental scale, and mapped the difference in forest structure potential from 1960 to 2012. Throughout this analysis, we quantified the absolute biophysical upper limits of each forest structure as dictated by its climate alone. Whether a forest is managed or unmanaged, young or old, the potential forest structures as defined by its climate will not change unless its climate changes or substantial genetic mutations occur that influence the biophysics of trees, or new species evolve.

2.2. Forest structure data

We are defining forest structure as forest attributes that dictate the physical structure of a forest. In this case, we are focusing on canopy height, average diameter at breast height and basal area. Our forest structure data is derived from the largest harmonized forest plot-level inventory data set in Europe which consists of 13 different countries and 261,465 plots from the years 2000 to 2010 (Moreno et al., 2016a; Neumann et al., 2016a). A hybrid k-means clustering and nearest neighbor approach was used to gap fill areas without National Forest Inventory (NFI) data, as has been used in North America, individual countries in Europe, and on the global scale (S1) (Reese et al., 2003; Simard et al., 2011; Wilson et al., 2012; Beaudoin et al., 2014; Maselli et al., 2014; Crowther et al., 2015). This resulted in a pan-European spatially explicit data set of mean diameter at breast height (DBH), mean tree height and mean basal area per hectare on a 0.133° resolution representing the decade 2000 to 2010 (Fig. 2). DBH and height are mean values for all trees within a cell and do not represent individual tree values. Basal area is a measure of abundance of trees per hectare and can be used as a proxy for growing stock or tree carbon, with the advantage of being less affected by calculation procedures (Neumann et al., 2016b). We focus on these 3 variables because they are directly measured in the field and require little to no post processing which can be done differently throughout Europe. These 3 variables should be the most consistent forest attributes on forest structure from country to country.

The results for forest inventory plots were aggregated to a spatial resolution of 0.133° to maximize the reliability and accuracy of the output as well as the agreement with remotely sensed products (Moreno et al., 2016b). Next, we computed weighted averages for each cell with data, accounting for differences in sample design and grid distance across countries (Tomppo et al., 2010). We then gap-filled the cell-level data into areas that lack information using a combination of clustering and nearest neighbor analysis. This procedure utilized several remotely sensed and gridded data products (S2) resulting in unbiased pan-European estimates of forest structures that maintain continental scale variability (S3). We focused on diameter, height and basal area because they are the least dependent on post-field collection processing. For example, carbon and volume calculation methods vary greatly by country resulting in large differences (Neumann et al., 2016b).

2.3. Climate data

We used climate data from a downscaled European Observation (*E-OBS*) data set (Moreno and Hasenauer, 2015). This pan-European downscaled data provides daily climate information from 1950 to 2013 on a 0.0083° resolution, including minimum and maximum temperature and precipitation. To be comparable with the forest structure data, we spatially upscaled the climate data from its native resolution (0.0083°) by computing the average on a 0.133° resolution (Fig. 1). We computed decadal average values for each climate variable from the 1950s to the 2000s (1950–1959, 1960–1969, etc.) to quantify trends in recent climate conditions in Europe. All of the raw climate data can be obtained at ftp://palantir.boku.ac.at/Public/ClimateData. Additionally, a newer updated version of this Moreno climate data set is also now available.

2.4. Upper limit forest structure response to climate

We first analyzed how each of the three climate variables (maximum, minimum temperature and precipitation) affects the three forest structure variables (DBH, height and basal area) individually using the

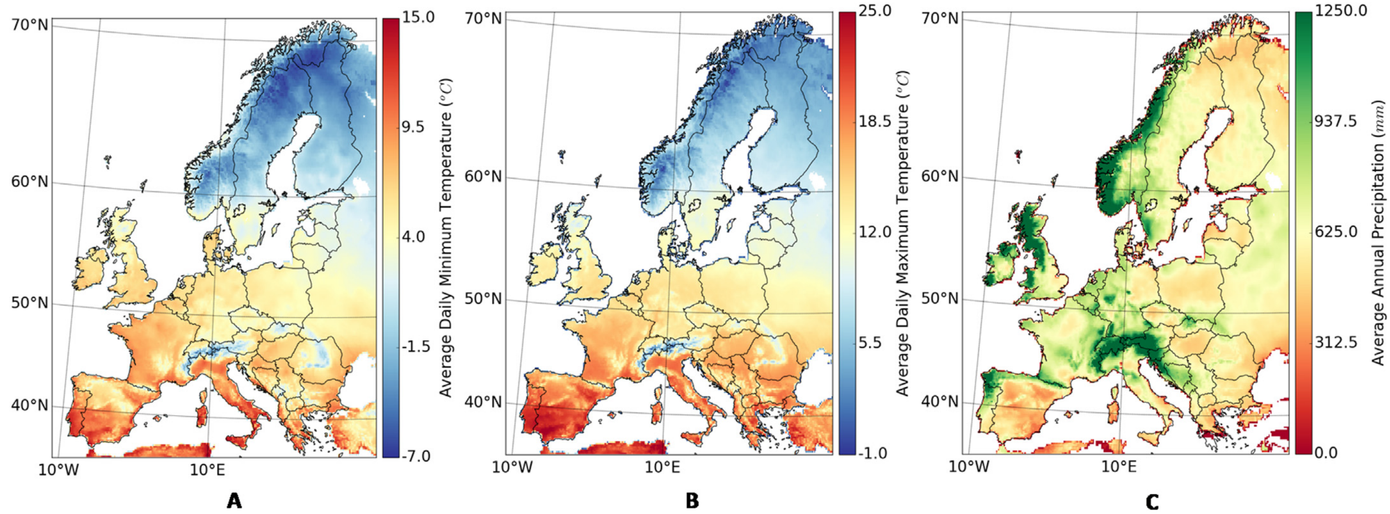

Fig. 1. Decadal mean climate data from 2000 to 2010. Minimum temperature (A), maximum temperature (B) and precipitation (C). Temperature is given as average daily values in °C and precipitation as average annual sums in mm.

daily averages over the decade of the 2000s. Then we analyzed how combinations of temperature and precipitation affect those same forest variables. We computed upper limits from groups of forests under the same climate conditions to quantify potential forest structure values under certain climate conditions (i.e., the highest level that can be reached under different climates). We defined the upper limit as the upper whisker in a box plot of each set of values from forests with the same climate conditions for each forest structure variable. For example, to obtain the forest structure limits for an average maximum temperature between 1 °C to 3 °C, we took each forest structure value where the decadal daily average maximum temperature is between 1 °C and 3 °C and placed them into the same group for analysis. The upper whisker (Eq. 1) represents the upper limit of forest structure variables under certain climate conditions, while disregarding outliers. We then plotted the results in upper limit response curve plots. We defined the upper whisker as:

$$Upper\ Whisker = Max(P_{75} + 1.5 * iqr) \tag{1}$$

$$iqr = P_{75} - P_{25} \tag{2}$$

P_{75} is the 75th percentile value of the forest structure group in question, P_{25} is the 25th percentile value and *iqr* the interquartile range. *Max*() is the maximum value from the data grouping that lies below the value within the parenthesis. We use all data available and do not limit results based on occurrence.

The upper limit values that we are quantifying include values from managed and unmanaged, and young and old forests. We are quantifying the absolute biophysical potential upper limit of forest structures, which may come from a managed or unmanaged forest or a young or old forest. As we are isolating only the climate effects on forest structure potential we do not parse our data by management or age. These curves represent the biophysical potential upper limit response to climate, which we assume will not have changed since the 1950's.

2.5. Forest structure in climate space

We created climate space plots to assess the limitations combinations of temperature and precipitation has on forest structure (Ohlemüller, 2011). Climate space refers to the fact that forest structures are plotted in relation to climate instead of geographic location. We performed a similar grouping as used for the upper limit curves, but instead using two climate variables instead of one. We did this for the combinations, minimum temperature and precipitation as well as maximum temperature and precipitation. Again, we computed the upper whisker values of each group.

2.6. Forest-level structure response to climate change

Changes in climate conditions will change the potential upper limit of forest structures. We plotted the decadal climate development of forest structure response for eight forests in the climate space plots from the 1950s to the 2000s. We selected these forests to cover our study's geographic range and the range of climate values (Table 1, Fig. 2). For each forest, we tracked their location in climate space as they progress through time.

2.7. European-scale forest structure limits and response to climate change

We used our upper limit response curves to map the upper limits geographically, to visualize how climate limits forest structure. This resulted in spatially explicit data sets of potential upper limit forest structure values. To accomplish this, for each cell, for each forest structure, based on its climate conditions in the 2000s, we mapped the values of the lowest upper limits found in the three upper limit response curves. For example, one particular cell in our map might have an average minimum temperature of 1 °C, an average maximum temperature of 10 °C and 1000 mm of average annual precipitation from 2000 to 2010. We then take these three values and use the upper limit response curves for each forest structure, for example DBH, to determine which response curve has the lowest DBH upper limit value given this cells climate conditions. The lowest value found is placed on the map. We also mapped which climate variable resulted in the lowest upper limit value indicating which climate factor is the most limiting on each forest structure variable. If two climate variables resulted in nearly

Table 1
Forests and their locations used in analysis in this study.

Forest Name	Country	Latitude	Longitude
The Black Forest	Germany	47.8413 N	7.9607 E
Doñana National Park	Spain	37.1899 N	6.4127 W
Lemmenjoki National Park	Finland	68.6388 N	25.5985 E
Söderåsen National Park	Sweden	56.0260 N	13.2325 E
Białowieża Forest	Poland	52.7228 N	23.6555 E
Landes de Gascogne Regional Natural Park	France	44.5000 N	0.8332 W
Galloway Forest Park	United Kingdom	55.1238 N	4.4241 W
Ålfotbreen Fjords	Norway	61.7352 N	5.6839 E

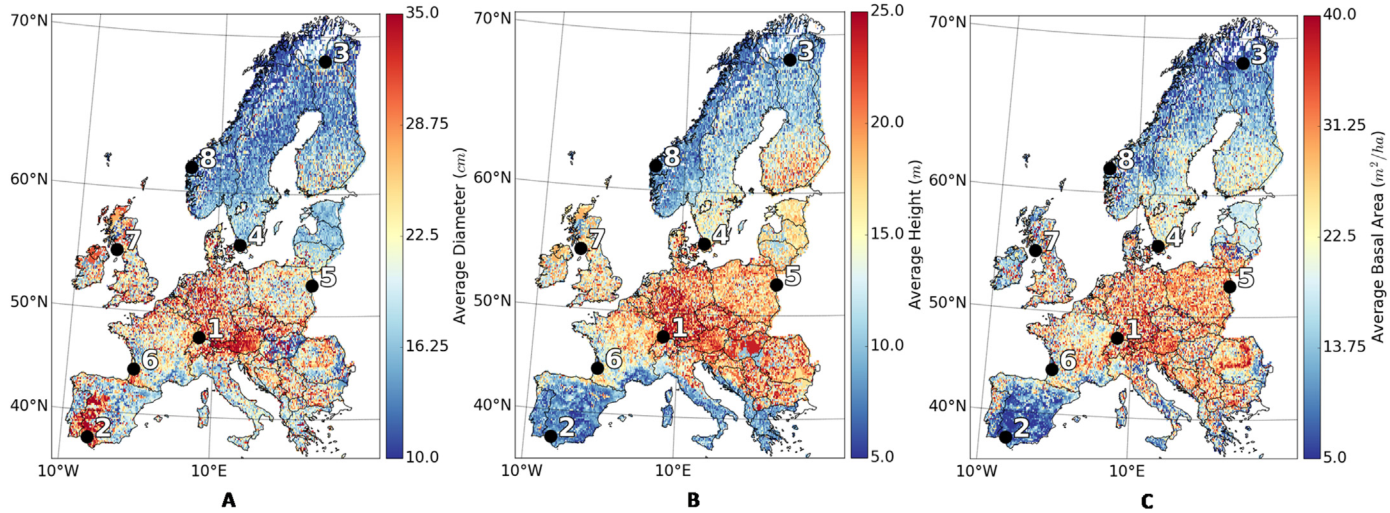

Fig. 2. Forest structure data for average tree height (A), average diameter (B) and average basal area (C). Dots and numbers indicate individual forests used in this study. 1) The Black Forest in Germany, 2)Doñana National Park in Spain, 3) Lemmenjoki National Park in Finland, 4) Söderåsen National Park in Sweden, 5) Białowieża Forest in Poland, 6) Landes de Gascogne Regional Natural Park in France, 7) Galloway Forest Park in The United Kingdom and 8) The fjords around Ålfotbreen in Norway. Data comes from Moreno et al. (2016a)

the same lowest upper limit value than we indicate that this location is limited by two climate variables equally. We produced the same potential maps using 1960's climate data and then found the difference in potential between then and recent years to analyze how Europe's changing climate may have altered forest structure potentials on a continental scale. Here, we use the 1960's instead of the 1950's because the climate data for the 1950's has large spatial holes found in the original E-OBS.

3. Results

3.1. Upper limit forest structure response to climate

We first analyzed how single climate variables affect the absolute biophysical upper limits of forest structures (Fig. 3). These upper limit values represent the upper limit of the mean within a cell and not the upper limit of individual trees. Each cell represents 0.133° or approximately 16x16km though the area varies with latitude. Tree height upper limits respond similarly to diameter with all three climate variables (Fig. 3, top row). Several tree height maxima are evident at −0.7 °C, at 17.9 °C and 25.7 °C. Though similarities exist between the diameter and height patterns with respect to maximum temperature, diameter tends to maintain high values with increasing minimum temperature where height tends to decrease. Precipitation affects diameter and height similarly with a tipping point at 1900 mm where they both rapidly decrease.

Basal area exhibits a parabolic, unimodal distribution for all climate variables. The lowest basal area (20–30 m^2/ha) is found at both extremes of the range of climate conditions. Minimum temperature shows a symmetrical pattern with an increase of about 3 m^2/ha per increase of 1 °C until 4 °C and a decrease of 3 m^2/ha until the end of the range. Maximum temperature and precipitation show a less uniform pattern. Between 19 and 21 °C maximum temperature, basal area drops from 40 to 15 m^2/ha (−63%), and with precipitation of 2000 to 2200 mm there is a drop by 20 m^2/ha or 40%.

3.2. Forest structure in climate space

As climate variables affect ecosystems in conjunction with one another, we analyzed how temperature and precipitation, taken together, limit forest structures. For this reason, we plotted potential upper limit forest structures in the climate space of minimum temperature and precipitation (left column in Fig. 4) as well as maximum temperature and precipitation (right column in Fig. 4). Previous research has also used the idea of climate space to study various aspects of forests (Smith et al., 2008; Ohlemüller, 2011; Wiens et al., 2011).

The shape of the climate space plots are a result of the combinations of temperatures and precipitation that we found in our European climate data (Fig. 4). Europe climate space exhibits a triangle shape and demonstrates how temperature and precipitation limit one another. As precipitation increases, the variability in temperature decreases, resulting in a narrow range of temperatures at high precipitations. This is not to say that if combinations of temperature and precipitation do not appear in our climate space plots that they cannot exist at all; it simply means that they are not found in our climate data representing the European decadal average values from 2000 to 2010.

The climate space plots have similar forest structure patterns for all three forest structure variables with slight differences (Fig. 4). The highest values for all forest structure variables can be observed in the center of the European climate space plots, and the lowest values are commonly found around the borders. Only diameter shows a bimodal distribution, with an additional maximum at warm and dry conditions, common to Mediterranean forests. These patterns are also reflected in the single variable upper limit curves (Fig. 3).

Basal area and tree height show a more pronounced ridge line than diameter with maximum values ranging from moderate, dry (7 °C, 500 mm) to cooler, wetter conditions (2 °C, 1500 mm; Fig. 4). Basal area also demonstrates a broader zone of moderate values than height or diameter. Basal area has more moderate values extending into the cold/dry and the warm/wet regions than other structures. Diameter is shown to be more limited by lower temperatures than by higher temperatures. Height values have a steeper response to climate as shown by the absence of green values as compared to the other structure variables.

3.3. Forest-level structure response to climate change

Spatially-explicit forest structure data along with temporally and spatially explicit climate data allows us to track how climate limits on forest structure have changed for individual forests through time. We chose 8 forests to track through time over our climate space (Fig. 4). All forests experienced a general increase in temperature. Precipitation, however, shows no clear pattern for the 8 analyzed forests. Regions seperated geographically can maintain the same climate space as shown by the Black Forest in Germany and Galloway forest park in the United

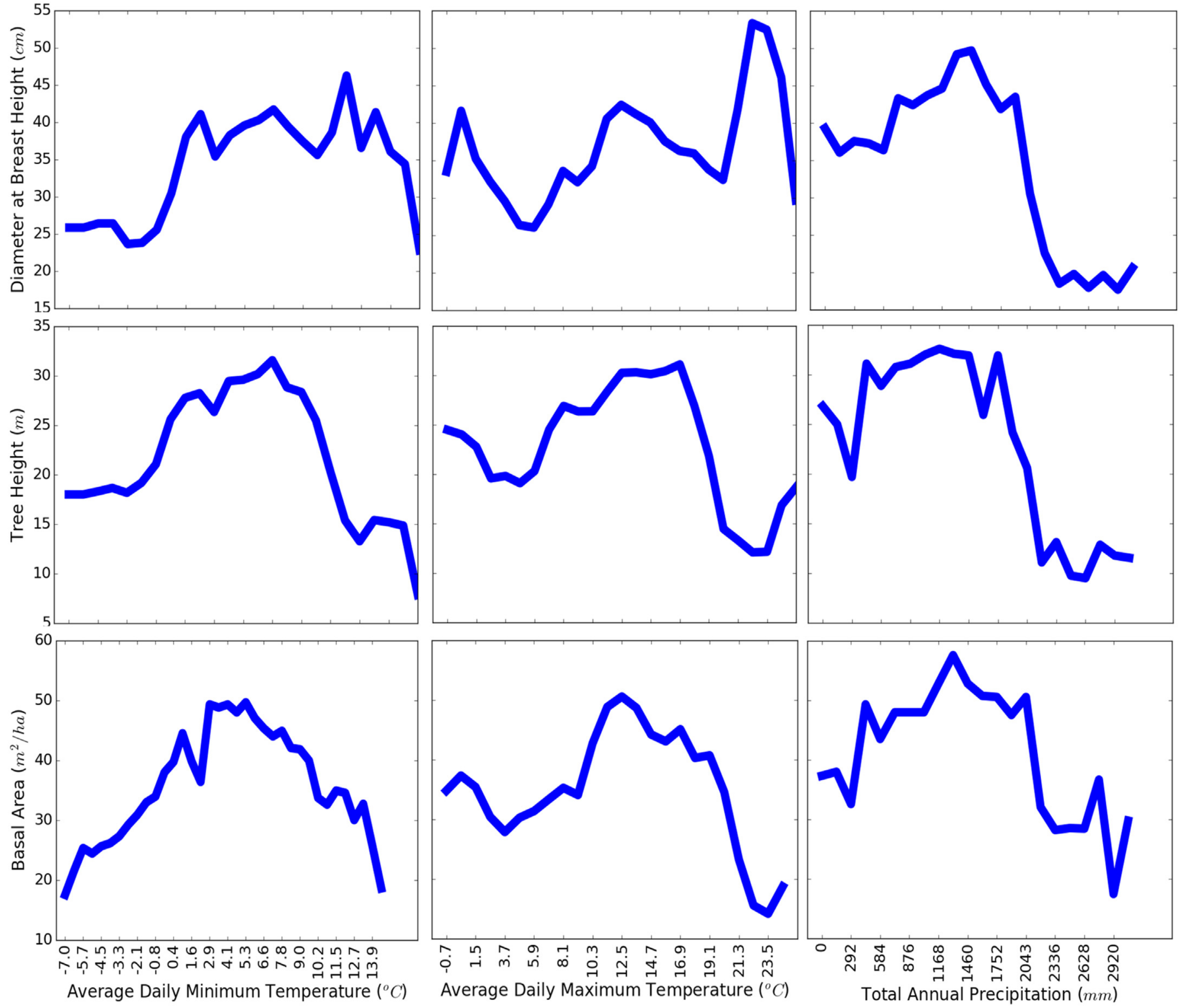

Fig. 3. Upper limit response curves of forest structure (rows) to decadal climate averages (columns) across Europe.

Kingdom. Lemmenjoki in Finland, Alfotbreen in Norway and Donana Nationalpark in Spain are located at the 3 pinnacles of our European climate space triangle. While the climate conditions in Spain did not show a clear shift in any direction, the forests in Finland and Norway experienced strong changes in climate conditons since the 1950s (Alfotbreen – increased in precipitation by about 400 mm, Lemmenjoki - increased in minimum temperature by 3 °C). The Lemmenjoki forest in Finland had climate conditions in the 1950s that no longer exist in our current climate space plot.

As these forests' climate changed, the potential upper limits of their various forest structures also changed. Some forests like Galloway and Landes de Gascogne in France were in the zone of high forest structure values in the past, but now lie outside of this zone. Other forests, such as Białowieża in Poland and Söderåsen in Sweden began outside the high value zone but moved into high values with climate change. We can also see that a forests' minimum and maximum temperature limits its potential differently. Basal area for Söderåsen in the 1950s is in the high value zone in the minimum temperature/precipitation plot, but not in the maximum temperature/precipitation plot indicating that Söderåsen was more limited by maximum temperature than minimum temperature.

3.4. European-scale forest structure limits and response to climate change

We then performed our climate space analysis in reverse by placing the potential upper limit values back on the geographic map to analyze how climate limits forest structure geographically. The results are gridded data sets of potential upper limit forest structures. We also plotted which climate factors are the most limiting on each structure spatially. Each forest structure has a different geographic pattern (Fig. 5). For example, Spain can support high average diameters while it only supports shorter forests with less basal area as compared to the rest of the continent. The climate factors that are dictating these forest structure limits vary spatially as well as between forest structures; For example in large areas of France DBH is most limited by minimum temperatures, height by precipitation and basal area by maximum temperatures.

Climate has changed over the last few decades (Fig. 6). This change is not uniform over Europe. In general, nearly all of Europe has experienced increased minimum and maximum temperatures, but at

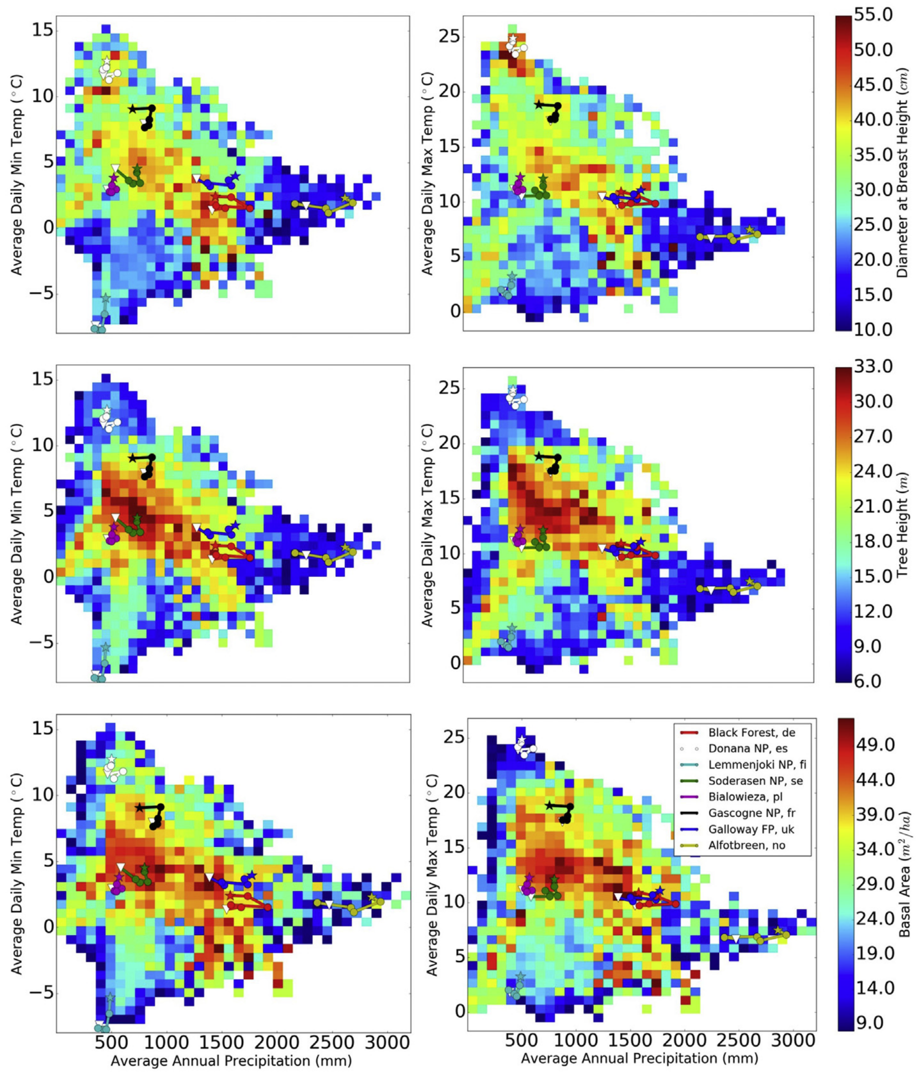

Fig. 4. Potential forest structures in climate space. Left column is minimum temperature versus precipitation and right column is maximum temperature versus precipitation. First row represents diameter at breast height, second average tree height, and third basal area. Eight individual forests and their climate progression through time are shown. Each mark represents decadal averages from 1950 to the 2000s. The white triangle indicates the 1950s and the star represents the 2000s.

different rates. Precipitation trends are not as ubiquitous as the majority of southern Europe has become drier, while the majority of northern Europe experienced increased precipitation (Fig. 6) (Moreno and Hasenauer, 2015).

To see how this changing climate affects not only individual forests on the local level, but impacts all forests on the continental scale, we plotted the difference in potential forest structure when using the 1960s climate compared to potential when using current climate conditions (Fig. 7). Overall, Europe experienced decreases of 5.0%, 1.7% and 6.5% in diameter, height and basal area potential respectively. However, this decrease is not constant over the entire landscape. The majority of Europe, especially throughout central Europe experienced relatively little change compared to the rest of the continent. Some areas, like the Iberian Peninsula have experienced high levels of change in potential upper limits. These maps show which forests will have greater capacity to maintain larger, taller and more expansive forests, and which are losing capacity. No latitudinal pattern is shown in increasing or decreasing values. Additionally, change is not consistent across elevational gradients. The Austrian and Swiss Alps have a general decrease in values while the Pyrenees experienced an increase or no change.

4. Discussion

Climate clearly places limits on forest structures as shown by our response curves and climate space plots (Fig. 3; Fig. 4). Of course, other aspects of the environment also limit forest structure such as soil, management and disturbance regimes. We assume that over the entire continent for each climate grouping, a range of forest conditions will exist. This assumption may only be made when using very large and spatially extensive data sets. We have infromation estimating climate and forest structure for every forest in Europe. That is to say, our data contains forests that experience intensive managment and those being conserved, are strongly limited by soils and are not limited by soils, and with frequent disturbance regimes and those with infrequent disturbances. We, however, isolate the impact climate has on forest structure by using this big-data principle to assume that within each group we will encounter a forest whose management type and site conditions are not the limiting factor; leaving climate the limiting factor to a forest structure. We took the upper whisker value for every climate grouping, for each forest structure in our analysis, to capture the value of each forest structure variable that is primarily limited by climate.

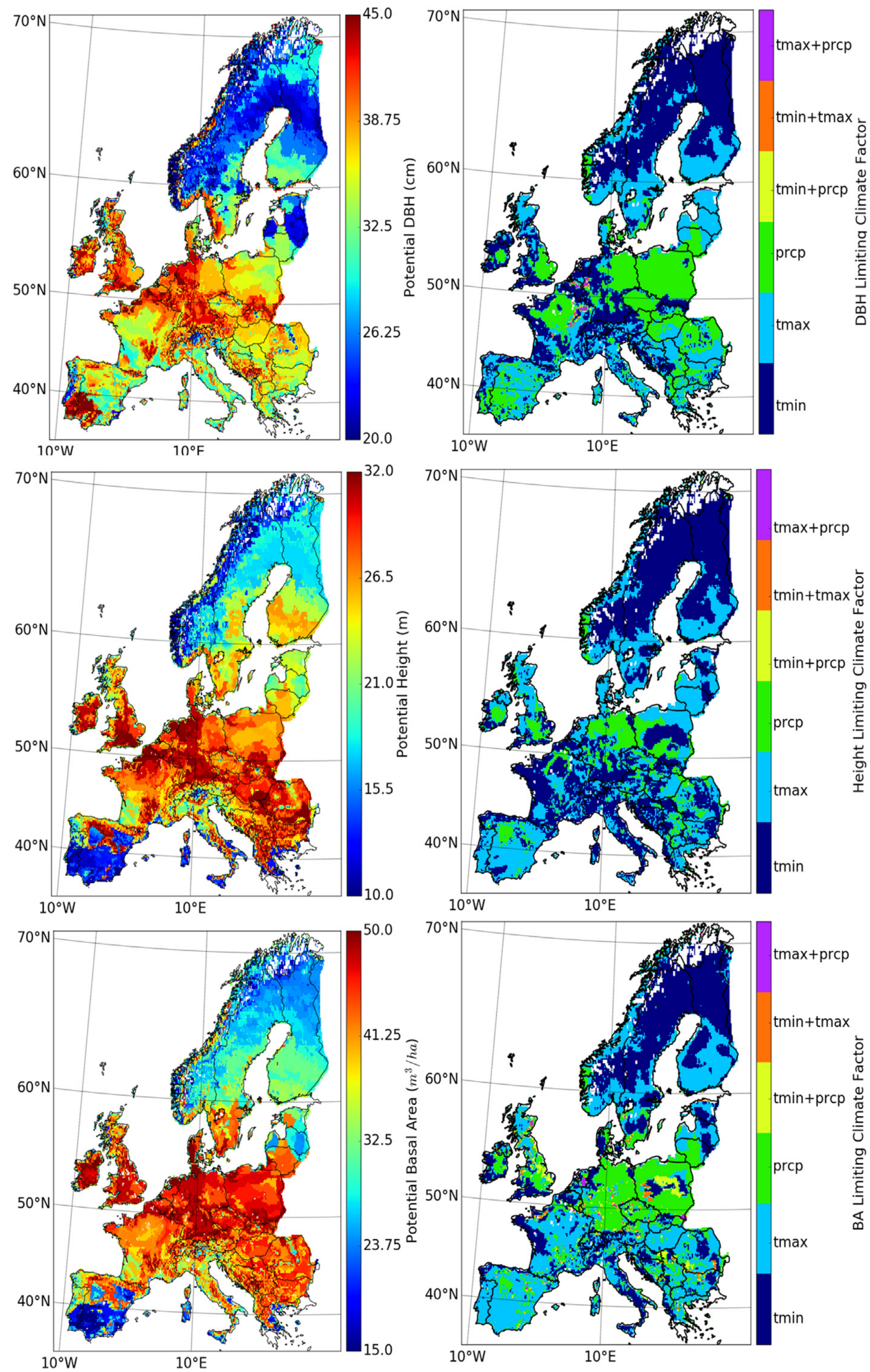

Fig. 5. Upper limit potentials for diameter, height and basal area along with the most limiting climate factors.

4.1. Climate limits on forest structure

The upper limit response curves for basal area indicate a somewhat parabolic pattern response to all three climate variables, with minimum temperature having the clearest signal which demonstrates an optimal minimum temperature for basal area (Fig. 3). This means that for a forest to have the highest basal area values in Europe it is required that the forest have this minimum temperature. Towards the high minimum or maximum temperatures, basal area becomes highly limited. This does not necessarily equate to arid areas having the most limited basal area. High precipitation limits basal area more than low precipitation. This results from the temperate nature of climate in Europe. High temperatures with high precipitation that may support high basal areas do not exist in Europe, demostrated by our climate space plots (Fig. 4). The linear downward pointing ridge in high basal area values in the minimum temperature/precipitation climate space plot is a result of mountain ranges (Fig. 4). This zone of high values is also present in the DBH and height climate space plots. These alpine zones exist throughout Europe and demonstrate a wide spectrum of climates from the Mediterranean and temperate Alps, to the boreal mountains of Norway. Common to all of these mountain ranges are high forest structure potential upper limit values (Fig. 4).

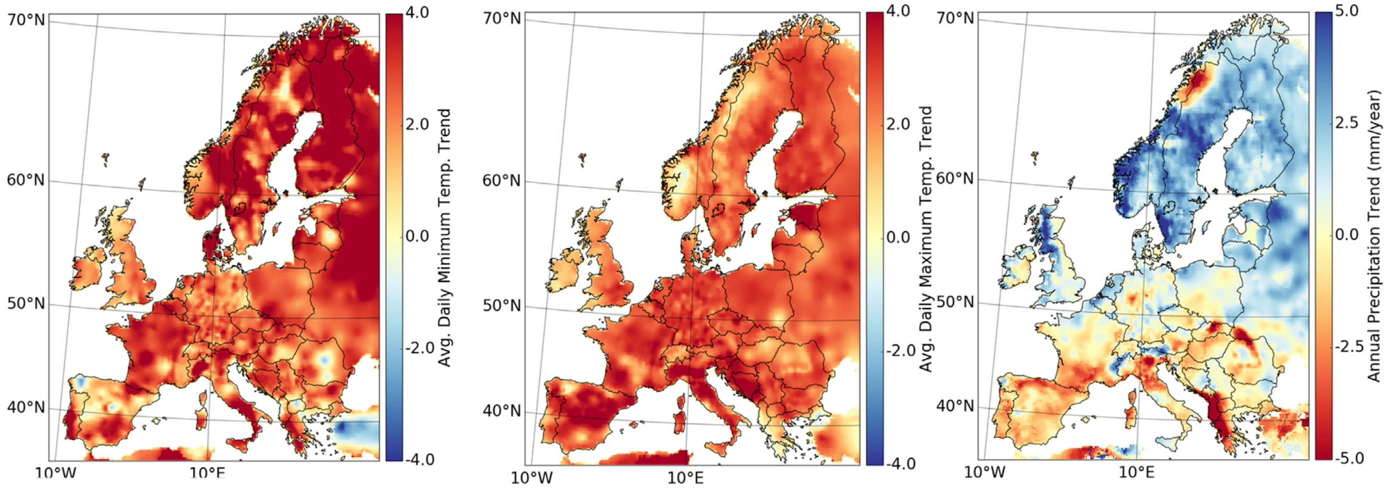

Fig. 6. Climate trends from 1950 to 2010. Trend value represents slope of a linear fit over all annual averages. Temperature is in 1/100 of a degree per year (for example, 4/100 * 60 years = 2.4 °C increase). Precipitation is in mm/year.

Height and DBH behave similarly in respose to climate (Fig. 3); which is to be expected as it has been shown that they have a strong allometric relationship (Niklas, 1995). However, the small differences in the upper limit response curves result in more pronounced differences in the climate space plots (Fig. 3; Fig. 4). The DBH climate space plots have a less pronounced zone of high values than height. However, DBH has more moderate to high values given high and low temperatures. This is corroborated by arid forests often being able to support short and wide species of trees, such as juniper, various oaks and pines. The physiological principle known as Darcy's Law states that temperature and precipitation must limit the height of trees, whereas no such known principle exists for diameter (McDowell and Allen, 2015).

A zone of moderate values exists in climate space, starting in the middle of the climate space plots and pointing down and to the left in the minimum temperature/precipitation plots. These areas are typically found in and around Finland. Finland receives less precipitation than the rest of Scandinavia, and from our upper limit curves we see that, when not limited primarily by high temperatures, lower precipitation leads to taller forests. These climate conditions allow Finland to support taller forests than its wetter Scandinavian neighbors.

In both the upper limit response curves and climate space plots, tipping points are evident. Tipping points here refer to climate values along the upper limit response curves or locations in climate space that thereafter result in rapid changes to forest structure (Fig. 3,Fig. 4). These tipping points can result in increases in upper limit values such as in DBH at 0.0 °C minimum temperature or decreases as with all three forest structures at approximately 2000 mm precipitation. These tipping points demonstrate ecological thresholds that result in the varying forest types found across climatic zones. The line graphs show the rapid shifts that can be found in landscapes when transitioning from one climatic zone to another. For example, the minimum tempearture impact on basal area graph (Fig. 3) can be related to descending a mountain. Typically, the highest elevation summits will have low basal areas and the lowest minimum temperatures but then the basal area increases as one descends. However, this increase reverses as one approaches a valley which has the highest minimum temperatures. Quantified values for tipping points to structure change provides valuable information to policy makers in the context of a changing climate, especially if their forests have climate conditions close to these tipping points.

Geographic spatial patterns of climate limitations on forest structures clearly emerge when forest structure potentials are plotted geographically (Fig. 5). Our geographic potential plots show that forest structures are not all limited in the same ways spatially. A clear example of how structures are limited differently in the same location is southwestern Spain. Here, DBHs can become high in comparison with the rest of Europe, while heights and basal area potentials remain low. Heights in this case are primarily limited by maximum temperatures.

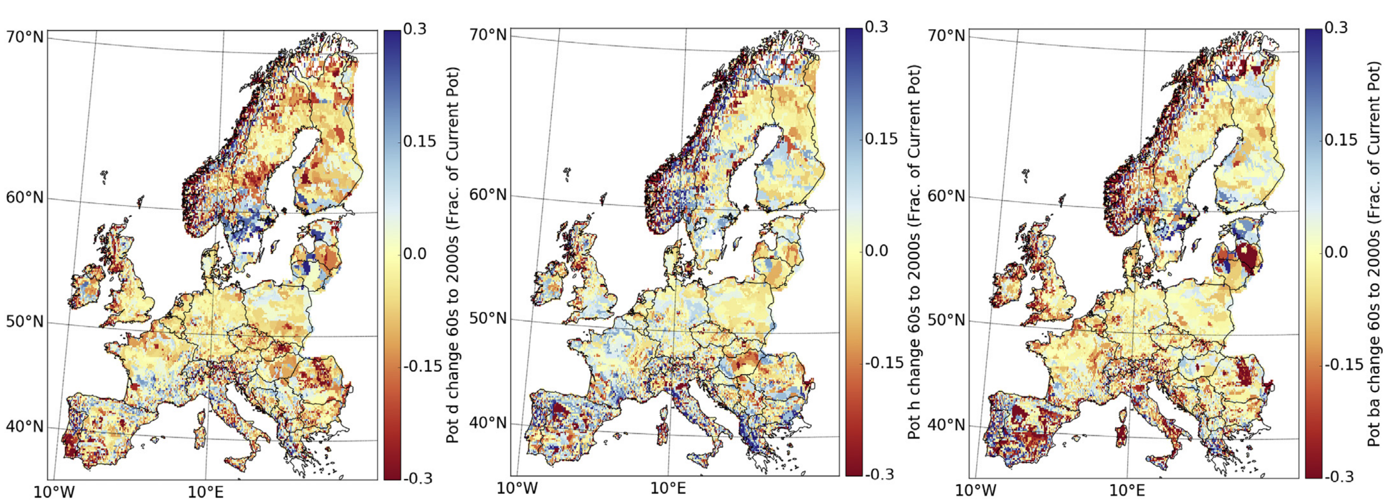

Fig. 7. Change in upper limit potential for diameter at breast height, height and basal area from the 1960s to the 2000s.

This again agrees with Darcy's Law which states that height must be limited by the hydraulic potential, or vapor presure deficit, which in turn is exponentially impacted by temperature in drier areas (McDowell and Allen, 2015).

Precipitation can limit forest structure by being either too low, as is seen throughout the Mediterranean, or too high, as exemplified by the British Isles (Fig. 5). In the British Isles precipitation limits all three forest structures. This effect is shown by our upper limit curves (Fig. 3). The high precipitation, however, might only be a correlated indicator with lack of solar radiation being the primary limiting factor. Whether the excessive precipitation or the lack of solar radiation caused by clouds which accompany precipitation is the true limiting factor, the presence of precipitation is the driver of the limitation.

Areas throughout central Europe, from the Alps to northern Germany, consistently have the highest potentials in all 3 forest structures with a mix of limiting climate factors. This indicates that these areas have ideal climatic conditions, in Europe, for maximizing DBH, height and basal area. This follows that these areas also have the largest growing stock in Europe, excluding Russia (EU commission, 2011). However, current growing stock is not a good measure of forest structure potential as shown in the British Isles, which have high potential values in all three forest structures but have low growing stocks. This would indicate that, if not limited by some other environmental factor, a change in forest management in the British Isles could result in forests similar to the forest with highest growing stock in Europe.

4.2. How climate change has affected forest structure

We assumed that the upper limits for each temperature/precipitation grouping will not change through time; that is to say that the biophysics that govern forests will not have changed since the 1950's. Using this assumption we plotted 8 forest's climate development through time on our climate space plots (Fig. 4). Changes in climate from 1950 to 2012 have had an impact on forest structure potential on the individual forest level (Fig. 4). The 8 forests we plotted on our climate space plots demonstrate different patterns through time (Fig. 4). Some forests show little change like Doñana National Park in Spain, and Białowieża Forest in Poland. In the case of Doñana NP this could be because it is approaching the limits of Europe's current climate space, which may in turn be limited by some other factor like atmospheric CO_2 concentrations (Norby et al., 2010). In the 1950s, in the minimum temperature/precipitation plot, Lemmenjoki National Park in Finland existed in a climate space that no longer exists in Europe. This exemplifies the evolving nature of climate space through time. As minimum temperatures rose, the very coldest minimum temperatures in Europe began to vanish, until today where this whole area of climate space is now gone. This shows how habitats for sensitive species that require very specific climate conditions can vanish on an entire continent. The repercussions of these vanishing habitats on the borders of our climate space may lead to species extinction because the necessary climate conditions can no longer be found on this continent.

The fjords around Alfotbreen in Norway experienced the greatest overall change in climate space as a result of increasing precipitation, however, the consequences of this shift in terms of forest structure are not as great as other forests that move shorter distances in climate space. From where Alfotbreen began in the 1950s, its DBH, height and basal area, potentials are similar to what they are in the 2000s. Some forests show a positive response to this shift, in terms of having less limited forest structures while others show negative effects. Söderåsen National Park in Sweden demonstrates a positive impact from its movement through climate space. In the 1950s Söderåsen was limited primarily by maximum temperatures. However, as temperature rose and precipitation increased, Söderåsen moved into the high value zone indicating that it became less limited by maximum temperatures and became one of the lesser climate limited forests in our study. Landes de Gascogne Regional Natural Park in France, however, shows a negative response to this shifiting climate as it moves towards a Mediterranean bioregion. This could have economic consequences because the large commercial plantations surrounding this forest, which may actually be close to their potential, will suffer the same fate. Since the 1950s, this area has experienced increased temperatures and decreasing precipitation, which in turn has moved it away from the high value zone which it had approached in the 1950s, for all forest structures. These forests represent only a few stands throughout Europe and were chosen to represent the extremes in our climate data and also well know recreational areas. Other forests would certainly show varying results. This is the limitation in examining only case studies. It is for this reason we also examined Europe as a whole.

Climate change since the 1960s has changed the forest structure potentials throughout all of Europe (Fig. 6; Fig. 7). To come to this conclusion we again assumed that the upper limit response curves do not change over time (Fig. 3). Repeated long-term observations from NFI systems would be needed to prove this assumption definitively, however, limitations on NFI data accessibility in Europe prohibit such a validation (Tomppo and Schadauer, 2012). The largest spatially explicit NFI data set in Europe only has repeated observations after the year 2000 (Neumann et al., 2016a). Therefore, we assume the potential upper limit curves, and climate space plots are valid to assess forest structure potentials under different climate conditions during different time periods. This analysis, in other large forested areas that have more open data policies, such as in the United States, could test this assumption as we could then do large scale time-series analyses which cannot be done in Europe because of restrictions to the access of data.

Our continental study of the impacts of climate change from the 1960s to the 2000s shows an overall decrease in forest structure potentials (Fig. 7). That is to say that since the 1960s European forests have diminished potential to grow dense tall forests with wide trees. Basal area has decreased the most, at 6.5% continentally, indicating a lower carrying capacity of forests in Europe today as compared to 50 years ago. The Iberian Peninsula has experienced a relatively strong decrease in all 3 forest structure potentials over the last 50 years. This is primarily caused by rising maximum temperatures and decreasing precipitation. Areas such as southern Sweden and Norway have experienced a general increase in forest structure potential upper limits. Central Europe has experienced relatively little change for two reasons. The first is because, as compared to other areas in Europe, central Europe has experienced the most moderate change in climate, especially in precipitation (Fig. 6). For example, Poland has experienced very little change in all 3 forest structures (Fig. 7), and we determined that Poland's potentials are primarily limited by precipitation (Fig. 5). Therefore, because little change in precipitation happened in Poland, and Poland is most limited by precipitation, there should not be much change in potentials in Poland. The second reason that central Europe has experienced relatively little change in potential forest structure is because of this area's climate position on our upper limit response curves (Fig. 3). Climate in central Europe tends to be in the moderate range compared to other areas in Europe which are experiencing larger climatic shifts. Given a moderate range of temperatures and precipitation the upper limit response curves tend to plateau. This means that with slight changes in climate at moderate temperatures and precipitations, little change in forest structure will occur.

This analysis shows which area's forest structures are becoming less limited by climate, and which are becoming more limited. As forest structure impacts many dynamics within a forest, it follows that changes in forest structure potentials may also have ramifications on the dynamics within forests and therefore, on landscapes. For example, change in potential forest structure may affect large-scale forest mortality events. We show a decrease in forest structures on the Iberian Peninsula primarily caused by rising temperatures (Fig. 5; Fig. 7). This agrees with previous research showing that increases in tree mortality in this region are primarily caused by rising temperatures, more so than decreasing precipitation, and strongly influenced by the structure of the

forest (Ruiz-Benito et al., 2013). Using concepts from this study, if a forest has typically been close to the potential upper limits in forest structure, then a decrease in forest structure potential in this forest would lead us to assume that a mortality event must occur to balance the forest to fit within the new upper limit. This principle has been witnessed with respect to height in the southwestern U.S.A., which has a similar climate to the Iberian penninsula (McDowell and Allen, 2015). Conversely, in areas where potentials have increased, forests may begin to increase in economic value and have less frequent mortality events. However, improvements cannot be observed as easily as mortality events. Structural improvements take decades to develop as forests grow, gain value, change disturbance regimes and establish, but a mortality event can happen in a day.

5. Conclusion

Climate limits forest structure throughout Europe and changes in climate can affect the potential upper limits of individual forests and entire continents. Forest structure dictates habitats, biodiversity, and forest economic value. Analyzing forest structure as opposed to fluxes and pools adds a level of information that previous analyses cannot provide. Our potential upper limit values represent means for entire forest stands and do not represent the upper limits of individual trees. By demonstrating how climate limits different forest structures through time and space, especially in the context of current climate trends, we can better understand Europe's forest development and its ever-changing structure. This research can help policy makers concerned with species conservation, wildlife habitat or timber market values to make long term and large-scale planning decisions. Additionally, we specify the climate variable that is most limiting to various forest structures providing information s as to what can be expected from forests in the future if current climate trends continue. Further research is needed to test our hypothesis that this type of analysis could help with understanding large-scale mortality events. If it could, it would inform policy makers how to preserve overall ecosystem services by targeting specific forest structures that must be altered in specific ways to accommodate new potential upper limits; before nature does it for them in the form of a mortality event. This paper demonstrates a new big-data approach to landscape ecology. The methods used in this paper can further make use of the growing data in large scale global ecology to ask theoretical scientific biogeography questions.

The use of repeated forest structure observations on a continental scale are necessary to validate our assumption that the upper limits of forest structure based on climate constraints are consistent through time. Data to perform such an analysis in Europe does not presently exist. Repeating this analysis using repeated observations would allow for deeper insights into climate-forest structure interactions and allow us to test our assumptions. Expanding this research into other large forested areas may also help us in better understanding drivers to current changes in global forests, such as the increase in mortality rates seen in the western United States (van Mantgem et al., 2009). Additionally, the climate impacts on forest structure is an easier concept to visualize for the general public. Explaining the repercussions of climate change in terms of heights and diameters is more tangible and less esoteric than explaining decreases in NPP or total carbon stock. In this way, our research may also help bridge the scientific-public communications gap when discussing climate impacts on forest ecosystems. Telling the public that all of their tall trees may die is more impactful than explaining a decrease in NDVI. The forest structure and climate data used in this study can be obtained at https://doi.org/10.6084/m9.figshare.c.3463902 and ftp://palantir.boku.ac.at/Public/ClimateData/ respectively.

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Appendix A. Supplementary data

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References

Beaudoin, A., Bernier, P.Y., Guindon, L., et al., 2014. Mapping attributes of Canada ' s forests at moderate resolution through k NN and MODIS imagery. Can. J. For. Res. 532, 521–532.
Bekker, M.F., Taylor, A.H., 2010. Fire disturbance, Forest structure, and stand dynamics in montane forests of the southern cascades, Thousand Lakes wilderness, California, USA. Ecoscience 17, 59–72.
Berry, P.M., Dawson, T.P., Harrison, P.A., Pearson, R.G., 2002. Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. Glob. Ecol. Biogeogr. 11, 453–462.
Bolte, A., Hilbrig, L., Grundmann, B., Kampf, F., Brunet, J., Roloff, A., 2009. Climate change impacts on stand structure and competitive interactions in a southern Swedish spruce–beech forest. Eur. J. For. Res. 129, 261–276.
Cardinale, B.J., Duffy, J.E., Gonzalez, A., et al., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67.
Cramer, W., Bondeau, A., Woodward, F.I., et al., 2001. Global response of terrestrial ecosystem structure and function to CO 2 and climate change: results from six dynamic global vegetation models. Glob. Chang. Biol. 7, 357–373.
Crowther, T.W., Glick, H.B., Covey, K.R., et al., 2015. Mapping tree density at a global scale. Nature 525, 201–205.
Dale, V.H., Joyce, L.A., Mcnulty, S., et al., 2001. Climate change and Forest disturbances. Bioscience 51, 723.
Dullinger, S., Gattringer, A., Thuiller, W., et al., 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nat. Clim. Chang. 2, 619–622.
Easterling, D.R., 2000. Climate extremes: observations, Modeling, and impacts. Science 289, 2068–2074.
EU commission, 2011. State of Europe's Forests 2011 344 pp.
FOREST EUROPE, 2015. State of Europe's Forests 2015. 314.
Hirota, M., Holmgren, M., Van Nes, E.H., Scheffer, M., 2011. Global resilience of tropical forest and savanna to critical transitions. Science (New York, N.Y.) 334, 232–235.
Idso, S.B., Kimball, B.A., 1993. Tree growth in carbon dioxide enriched air and its implications for global carbon cycling and maximum levels of atmospheric CO 2. Glob. Biogeochem. Cycles 7, 537–555.
IPCC, 2013. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia VB, Y. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA 1535 pp.
Johnson, F.L., Risser, P.G., 1975. A quantitative comparison between an oak Forest and an oak savannah in Central Oklahoma. Southwest. Nat. 20, 75.
Katz, R., Brown, B., 1992. Extreme events in a a changing climate: variability is more important than averages. Clim. Chang. 21, 289–302.
Keith, H., Mackey, B.G., Lindenmayer, D.B., 2009. Re-evaluation of forest biomass carbon stocks and lessons from the world's most carbon-dense forests. In: Proceedings of the National Academy of Sciences of the United States of America. 106. pp. 11635–11640.
Kelly, A.E., Goulden, M.L., 2008. Rapid shifts in plant distribution with recent climate change. In: Proceedings of the National Academy of Sciences of the United States of America. 105. pp. 11823–11826.
Kolby Smith, W., Reed, S.C., Cleveland, C.C., et al., 2015. Large divergence of satellite and earth system model estimates of global terrestrial CO2 fertilization. Nat. Clim. Chang. 6, 306–310.
Larjavaara, M., 2014. The world's tallest trees grow in thermally similar climates. New Phytol. 202, 344–349.
Larjavaara, M., Muller-Landau, H.C., 2012. Temperature explains global variation in biomass among humid old-growth forests. Glob. Ecol. Biogeogr. 21, 998–1006.
Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable Forest management. Conserv. Biol. 14, 941–950.
Luterbacher, J., Dietrich, D., Xoplaki, E., Grosjean, M., Wanner, H., 2004. European seasonal and annual temperature variability, trends, and extremes since 1500. Science (New York, N.Y.) 303, 1499–1503.
Maselli, F., Chiesi, M., Mura, M., Marchetti, M., Corona, P., Chirici, G., 2014. Combination of optical and LiDAR satellite imagery with forest inventory data to improve wall-to-wall assessment of growing stock in Italy. Int. J. Appl. Earth Obs. Geoinf. 26, 377–386.
Mayle FE, Langstroth RP, Fisher R a, Meir P (2007) Long-term forest-savannah dynamics in the Bolivian Amazon: implications for conservation. Philosophical transactions of the Royal Society of London Series B, Biological sciences, 362, 291–307.
McDowell, N.G., Allen, C.D., 2015. Darcy's law predicts widespread forest mortality under climate warming. Nat. Clim. Chang. 5, 669–672.
Mclachlan, M., Clark, J., Manos, P., 2005. Molecular indicators of tree migration

capacitry under rapid climate change. Ecology 86, 2088–2098.
Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., Vorosmarty, C.J., Schloss, A.L., 1993. Global climate change and terrestrial net primary production. Nature 363, 234–240.
Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being: Synthesis. Island Press, Washington, DC 155 pp.
Moreno, A., Hasenauer, H., 2015. Spatial downscaling of European climate data. Int. J. Climatol. 36, 1444–1458.
Moreno, A., Neumann, M., Hasenauer, H., 2016a. Forest structures across Europe. Geosciences Data Journal 4, 17–28.
Moreno, A., Neumann, M., Hasenauer, H., 2016b. Optimal resolution for linking remotely sensed and Forest inventory data in Europe. Remote Sens. Environ. 183, 109–119.
Neumann, M., Moreno, A., Thurnher, C., et al., 2016a. Creating a regional MODIS satellite-driven net primary production dataset for European forests. Remote Sens. 8, 1–18.
Neumann, M., Moreno, A., Mues, V., et al., 2016b. Comparison of carbon estimation methods for European forests. For. Ecol. Manag. 361, 397–420.
Niklas, K.J., 1995. Size-dependent allometry of tree height, diameter and truck-taper. Ann. Bot. 75, 217–227.
Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E., McMurtrie, R.E., 2010. CO2 enhancement of forest productivity constrained by limited nitrogen availability. In: Proceedings of the National Academy of Sciences of the United States of America. 107. pp. 19368–19373.
Ohlemüller, R., 2011. Running out of climate space. Science (New York, N.Y.) 334, 613–614.
Oren, R., Ellsworth, D.S., Johnsen, K.H., et al., 2006. Soil fertility limits carbon sequestration by forest ecosystems in a CO 2 -enriched atmosphere. Nature 323, 1999–2002.
Pan, Y., Birdsey, R., Fang, J., et al., 2011. A large and persistent carbon sink in the World's forests. Science 333, 988–992.
Pardini, R., de Souza, S.M., Braga-Neto, R., Metzger, J.P., 2005. The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. Biol. Conserv. 124, 253–266.
Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
Pauli, H., Gottfried, M., Dullinger, S., et al., 2012. Recent plant diversity changes on Europe's mountain summits. Science 336, 353–355.
Reese, H., Nilsson, M., Pahlén, T.G., Hagner, O., Joyce, S., Tingelöf, U., 2003. Countrywide estimates of Forest variables using satellite data and field data from the National Forest Inventory. BioOne 32, 542–548.
Ruiz-Benito, P., Lines, E.R., Gomez-Aparicio, L., Zavala, M.A., Coomes, D.A., 2013. Patterns and Drivers of Tree Mortality in Iberian Forests: Climatic Effects Are Modified by Competition. PLoS ONE 8.
Saatchi, S.S., Harris, N.L., Brown, S., et al., 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. In: Proceedings of the National Academy of Sciences of the United States of America. 108. pp. 9899–9904.
Satake, A., Rudel, T.K., 2007. Modeling the forest transition: forest scarcity and ecosystem SERVICE hypotheses. Ecol. Appl. 17, 2024–2036.
Scheffer, M., Hirota, M., Holmgren, M., Van Nes, E.H., Chapin, F.S., 2012. Thresholds for boreal biome transitions. In: Proceedings of the National Academy of Sciences of the United States of America. 109. pp. 21384–21389.
Schröter, D., Cramer, W., Leemans, R., et al., 2005. Ecosystem Service supply and vulnerability to global change in Europe. Science 310, 1333–1338.
Seidl, R., Schelhaas, M.-J., Lexer, M.J., 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Glob. Chang. Biol. 17, 2842–2852.
Seidl, R., Schelhaas, M.-J., Rammer, W., Verkerk, P.J., 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nat. Clim. Chang. 4, 806–810.
Shore, T., Brooks, J.E., Stone, J.E., 2003. Mountain Pine Beetle Symposium: Challenges and Solutions. In: Information Report BC-X-399. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC, Kelowna, British Columbia 287 pp.
Simard, M., Pinto, N., Fisher, J., Baccini, A., 2011. Mapping forest canopy height globally with spaceborne lidar. Geophysical Research 116.
Smith, B., Prentice, I.C., Sykes, M.T., 2008. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Glob. Ecol. Biogeogr. 10, 621–637.
Thurner, M., Beer, C., Santoro, M., et al., 2014. Carbon stock and density of northern boreal and temperate forests. Glob. Ecol. Biogeogr. 23, 297–310.
Tomppo, E.O., Schadauer, K., 2012. Harmonization of national forest inventories in Europe: advances under cost action E43. For. Sci. 58, 191–200.
Tomppo, E., Gschwantner, T., Lawrence, M., et al., 2010. National forest inventories: Pathways for Common Reporting. pp. 541–553.
van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., et al., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.
Wiens, J.A., Seavy, N.E., Jongsomjit, D., 2011. Protected areas in climate space: what will the future bring? Biol. Conserv. 144, 2119–2125.
Wilson, J.S., Baker, P.J., 1998. Mitigating fire risk to late-successional forest reserves on the east slope of the Washington Cascade Range, USA. For. Ecol. Manag. 110, 59–75.
Wilson, B.T., Lister, A.J., Riemann, R.I., 2012. A nearest-neighbor imputation approach to mapping tree species over large areas using forest inventory plots and moderate resolution raster data. For. Ecol. Manag. 271, 182–198.
Zhao, M., Running, S.W., 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. Science (New York, N.Y.) 329, 940–943.